

Distribution Characteristics of Soil Phosphorus Fractions in Lichen Crusts at Different Slope Positions in the Gurbantunggut Desert (Postprint)

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Abstract

Sand ridges, as the fundamental topographic units of deserts, the surface hydrothermal environment at different slope positions profoundly influences the development and spatial distribution patterns of biological soil crusts. Lichen crusts are widely distributed on desert surfaces; however, scientific questions regarding how lichen crusts at different slope positions affect soil phosphorus cycling and what the key influencing factors are remain unclear. Based on this, this study takes the Gurbantunggut Desert as the research area and systematically analyzes the variation characteristics of phosphorus fractions and related enzyme activities in lichen crust layers and the underlying 0-5 cm soil at different slope positions. The results show that stable phosphorus (HCl-Pi, HCl-Po, HCl-Pi, and Residual-P) accounts for more than 75% of total phosphorus (TP) content in soils, followed by moderately unstable phosphorus (NaOH-Pi and NaOH-Po) and unstable phosphorus (Resin-P, NaHCO₃-Pi, and NaHCO₃-Po). Slope position has a significant effect on stable phosphorus, while soil layer has a significant effect on moderately unstable phosphorus ($P < 0.05$). The contents of stable phosphorus, TP, organic phosphorus (Po), and inorganic phosphorus (Pi) all exhibited that in the crust layer, the bottom slope was significantly higher than the east and west slopes, while in the underlying 0-5 cm soil, the west slope was significantly lower than the bottom and east slopes ($P < 0.05$). In contrast, the content of NaOH-Pi showed that in the crust layer, the east and west slopes were significantly higher than the bottom slope, and in the underlying 0-5 cm soil, the west slope was significantly higher than the east slope and bottom slope. Regarding soil enzymes, the east slope had the lowest alkaline phosphatase activity (ALP) and β -glucosidase activity (GC) in the crust layer and the highest in the underlying 0-5 cm soil. Random forest model analysis revealed that moisture and temperature variations induced by slope position were the most critical factors influencing the contents of unstable phosphorus

and stable phosphorus in lichen crust soils, respectively. This provides scientific support for enriching theories related to soil phosphorus cycling in desert ecosystems.

Full Text

Distribution Characteristics of Soil Phosphorus Fractions in Lichen Crusts at Different Slope Positions in the Gurbantunggut Desert

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Abstract

As the fundamental terrain unit of deserts, sand ridges create distinct surface water and thermal environments at different slope positions that profoundly influence the development and spatial distribution patterns of biological soil crusts. Lichen crusts are widely distributed across desert surfaces, yet scientific questions remain unclear regarding how lichen crusts at different slope positions affect soil phosphorus cycling and what the key influencing factors are. Based on this knowledge gap, this study systematically analyzed variations in phosphorus fractions and related enzyme activities in lichen crust layers and the underlying 0–5 cm soil across different slope positions in the Gurbantunggut Desert. Results demonstrated that stable phosphorus fractions (HCl-Pi, HHCl-Pi, HHCl-Po, and Residual-P) accounted for over 75% of total soil phosphorus, followed by moderately labile phosphorus (NaOH-Pi, NaOH-Po, NaHCO₃-Pi, and NaHCO₃-Po) and labile phosphorus (Resin-P). Slope position significantly affected stable phosphorus, while soil layer significantly impacted moderately labile phosphorus ($P < 0.05$). The contents of total phosphorus, organic phosphorus, inorganic phosphorus, and stable phosphorus all showed significantly higher values at the

slope bottom compared to east and west slopes in the crust layer, whereas in the 0–5 cm soil layer, the west slope showed significantly lower values than the slope bottom and east slope ($P < 0.05$). The contents of NaOH-Pi and NaOH-Po were significantly higher on east and west slopes than at the slope bottom in the crust layer, while in the 0–5 cm soil layer, the west slope showed significantly higher values than the east slope and slope bottom. Regarding soil enzymes, the east slope exhibited the lowest alkaline phosphatase (ALP) and β -glucosidase (GC) activities in the crust layer but the highest activities in the underlying 0–5 cm soil. Random forest model analysis revealed that moisture and temperature variations induced by slope position were the most critical factors influencing labile and stable phosphorus contents in lichen crust soils, respectively. These findings provide scientific support for enriching theoretical frameworks of soil phosphorus cycling in desert ecosystems.

Keywords: biological soil crusts; lichen crusts; phosphorus cycling; temperate desert; slope position; Gurbantungut Desert

Phosphorus, as a key component of plant cell membranes, nucleic acids, and energy transfer systems, represents one of the most critical limiting nutrients affecting terrestrial ecosystem productivity. Soil phosphorus primarily originates from parent material weathering and minor atmospheric deposition, yet most exists in occluded forms that are difficult for plants to utilize. Based on its chemical form in soil, phosphorus can be divided into organic phosphorus (Po) and inorganic phosphorus (Pi), and further categorized according to bioavailability into labile phosphorus, moderately labile phosphorus, and stable phosphorus. Different phosphorus fractions exhibit significant differences in plant availability. Labile phosphorus can typically be directly absorbed by plants in the short term, moderately labile phosphorus is readily adsorbed and fixed by minerals such as iron and aluminum oxides and requires biological processes (soil extracellular enzymes, organic acids) or abiotic processes (H^+ ions) for conversion to labile forms before plant uptake, while stable phosphorus is difficult for plants to directly utilize and may require centuries to millennia for transformation.

In desert ecosystems, traditional stoichiometric analysis based on total nitrogen to total phosphorus ratios suggests nitrogen limitation and abundant phosphorus availability, which has somewhat constrained research development on soil phosphorus cycling in these systems. However, although total phosphorus content may be high, bioavailable phosphorus that plants can directly utilize remains low, severely limiting primary productivity in desert ecosystems. Therefore, investigating the composition and influencing factors of various soil phosphorus fractions is crucial for understanding stability maintenance mechanisms and sustainable development in desert ecosystems.

Soil phosphorus transformation is jointly influenced by abiotic and biotic factors. Among abiotic factors, geochemical processes and climate (temperature, precipitation, etc.) profoundly affect soil phosphorus transformation. Geo-

chemical processes control phosphorus fraction conversion through weathering, adsorption-desorption, and dissolution-precipitation reactions. Elevated temperatures promote the conversion of labile and moderately labile phosphorus to stable forms, while increased moisture from precipitation enhances metal ion diffusion and pH changes, affecting desorption, dissolution-precipitation processes, and ultimately phosphorus bioavailability. Beyond direct effects, temperature and precipitation also indirectly influence soil phosphorus cycling by affecting surface vegetation and soil microorganisms. Biotic factors such as plants and microorganisms regulate soil phosphorus through litter production, microbial biomass, and secretion of extracellular enzymes and organic acids. When experiencing phosphorus limitation, plants and microorganisms release phosphatases to mineralize Po or release organic acids to convert recalcitrant Pi into bioavailable forms, thereby enhancing phosphorus bioavailability.

In desert ecosystems, scarce precipitation prevents phosphorus leaching to deeper layers, making surface biological activity the primary determinant of phosphorus dynamics. Biological soil crusts, as important carriers of surface life activities in arid regions, are organic complexes formed by cryptogamic plants (cyanobacteria, lichens, mosses) cemented with soil surface particles. In some arid regions, crust coverage can exceed 70% of the surface area, improving hydrological processes, microbial activity, and promoting nutrient cycling of carbon, nitrogen, and phosphorus. Through crust succession, lichen crusts become widely distributed in deserts, accounting for approximately 40% of global terrestrial biological crust coverage. Lichen crusts penetrate the desert surface through rhizines and hyphae, fixing surface particles, and their rough, uneven surfaces promote rock weathering and subsequent phosphorus accumulation. Sand ridges, as fundamental desert terrain units, alter soil physicochemical properties through different slope-specific water and thermal environments, thereby influencing biological soil crust development and spatial distribution patterns. Previous research indicates that compared to east slopes, biological soil crusts on west slopes better utilize early morning condensation water for growth. However, how slope position affects phosphorus cycling in lichen crusts and the underlying mechanisms remain unclear.

Therefore, we propose two scientific hypotheses: (1) Environmental differences induced by slope position affect soil phosphorus fractions in lichen crusts, with higher phosphorus availability on west slopes compared to east slopes; and (2) Biotic factors are key determinants of phosphorus cycling in crust layers, while abiotic factors dominate in sub-crust soils. To test these hypotheses, we conducted this study in the Gurbantunggut Desert—the largest fixed and semi-fixed desert in China—using lichen crusts as our research object. We collected samples from lichen crust layers and underlying 0–5 cm soils at different slope positions to investigate how slope position influences soil phosphorus fraction characteristics, providing theoretical support for understanding soil phosphorus cycling in desert ecosystems.

1.1 Study Area Overview

The study area is located in the hinterland of the Gurbantunggut Desert within the Junggar Basin (44°15'–46°50' N, 84°50'–91°20' E), covering an area of 4.88×10^4 km². As China's second-largest desert and the largest fixed-semi-fixed desert, it is dominated by north-south trending linear sand ridges under the influence of westerly circulation, along with honeycomb and crescent dunes. The region experiences a typical temperate continental climate with hot summers and cold, snowy winters, an annual mean temperature of 5–7°C, annual precipitation of 70–150 mm, annual evaporation exceeding 2000 mm, and a stable snow cover period of 100–150 days. Early spring snowmelt provides abundant water and thermal conditions for plant germination and growth. Dominant shrubs include *Haloxylon ammodendron*, *Haloxylon persicum*, *Calligonum mongolicum*, and *Artemisia ordosica*, while major herbaceous plants are *Erodium oxyrhinchum*, *Ceratocarpus arenarius*, and *Centaurea pulchella*. The desert also hosts well-developed biological soil crusts, including algal, lichen, and moss crusts, with lichen crusts being dominant and differentially distributed across dune slope positions.

1.2 Plot Establishment and Sampling

In July 2023, we selected typical north-south trending sand ridges within a long-term desert ecosystem monitoring plot in the Gurbantunggut Desert. We established three 100 m × 10 m sampling belts (parallel to the ridge direction) on west slopes, slope bottoms, and east slopes, respectively. Within each belt, we set up five 2 m × 2 m quadrats spaced >10 m apart. In each quadrat, we collected well-developed lichen crust samples and underlying 0–5 cm soil samples, totaling 90 samples. Samples were placed in ziplock bags, stored at 4°C, and transported to the laboratory for processing. Soil samples were thoroughly mixed, with one portion air-dried for determination of carbon, nitrogen, phosphorus content, soil moisture, pH, electrical conductivity, and phosphorus fractions; another portion was stored at -20°C for ammonium nitrogen, nitrate nitrogen, and enzyme activity analyses. Concurrently, soil temperature data at different slope positions were collected using long-term data loggers.

1.3 Chlorophyll Content Determination

We used the ethanol extraction method to determine chlorophyll content as a proxy for lichen crust biomass. Fresh lichen crust samples (1.00 g) were ground with 10 mL of 95% ethanol. The mixture was kept in darkness for 30 minutes, then centrifuged, and absorbance was measured at 665 nm, 649 nm, and 470 nm. Chlorophyll a (Chl a), chlorophyll b (Chl b), and total chlorophyll (Chl) concentrations were calculated using the following formulas:

$$\text{Chl a (mg} \cdot \text{L}^{-1}) = 13.95 \times A_{665} - 6.88 \times A_{649}$$

$$\text{Chl b (mg} \cdot \text{L}^{-1}) = 24.96 \times A_{649} - 7.32 \times A_{665}$$

$$\text{Chl (mg} \cdot \text{L}^{-1}) = \text{Chl a} + \text{Chl b}$$

where X is pigment content ($\text{mg} \cdot \text{g}^{-1}$), C is pigment concentration ($\text{mg} \cdot \text{L}^{-1}$), N is dilution factor, V is extraction volume (mL), and M is sample mass (g).

1.4 Soil Physicochemical Properties Determination

Soil moisture content was determined gravimetrically after oven-drying at 105°C . Soil pH and electrical conductivity (EC) were measured using a potentiometric method at a 1:2.5 soil-to-water ratio. Total carbon (TC) and total nitrogen (TN) were determined by combustion using a Multi N/C 3100 analyzer (Germany) after removing inorganic carbon with HCl. Total phosphorus (TP) was measured by molybdenum-antimony colorimetry, while available phosphorus (AP) was extracted with $0.5 \text{ mol} \cdot \text{L}^{-1} \text{ NaHCO}_3$ and measured colorimetrically. Ammonium nitrogen ($\text{NH}_4^+\text{-N}$) and nitrate nitrogen ($\text{NO}_3^-\text{-N}$) were analyzed using a continuous flow analyzer (Germany).

1.5 Soil Enzyme Activity Determination

We measured alkaline phosphatase (ALP) and β -glucosidase (GC) activities related to soil phosphorus cycling using commercial assay kits (Suzhou Grace Biotechnology Co. Ltd., Jiangsu, China). For ALP activity, soil samples were incubated with p-nitrophenyl phosphate under specific conditions, producing yellow p-nitrophenol that was measured colorimetrically at 405 nm. For GC activity, the enzyme catalyzed the hydrolysis of p-nitrophenyl- β -D-glucopyranoside to produce p-nitrophenol, which was measured at 400 nm. Enzyme activities were expressed as $\text{nmol} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$.

1.6 Soil Phosphorus Fractions Determination

We used a modified Hedley sequential extraction method to determine soil phosphorus fractions. Air-dried and homogenized soil samples were sieved through a 0.15 mm mesh, and 0.5 g subsamples were sequentially extracted with: (1) strong-base anion resin membrane (Resin-P); (2) $0.5 \text{ mol} \cdot \text{L}^{-1} \text{ NaHCO}_3$ ($\text{NaHCO}_3\text{-Pi}$ and $\text{NaHCO}_3\text{-Po}$); (3) $0.1 \text{ mol} \cdot \text{L}^{-1} \text{ NaOH}$ (NaOH-Pi and $\text{NaHCO}_3\text{-Po}$); (4) $1 \text{ mol} \cdot \text{L}^{-1} \text{ NaOH}$ (NaOH-Pi and NaOH-Po); (5) diluted HCl (HCl-Pi); and (6) concentrated $6 \text{ mol} \cdot \text{L}^{-1} \text{ HCl}$ (HHCl-Pi and HHCl-Po). Finally, the residue was digested with concentrated H_2SO_4 and HClO_4 to obtain residual phosphorus (Residual-P). All extracts were analyzed by molybdenum blue colorimetry. Organic phosphorus in each fraction was calculated as the difference between total and inorganic phosphorus. Based on previous research, phosphorus fractions were categorized into three groups: labile phosphorus (Resin-P,

NaHCO₃-Pi, NaHCO₃-Po), moderately labile phosphorus (NaOH-Pi, NaOH-Po, HCl-Pi), and stable phosphorus (HHCl-Pi, HHCl-Po, Residual-P).

1.7 Data Analysis

All data processing, statistical testing, and visualization were performed using R 4.1.2. Data normality and homogeneity of variance were verified to meet statistical assumptions. Two-way ANOVA was used to test the effects of slope position and soil layer on phosphorus fractions and enzyme activities, followed by least significant difference (LSD) tests for multiple comparisons. Pearson correlation analysis examined relationships between environmental factors, nutrients, and phosphorus fractions. Finally, random forest modeling identified key factors driving phosphorus fraction transformations using the randomForest package.

2.1 Soil Phosphorus Fraction Characteristics Across Slope Positions

Stable phosphorus (HCl-Pi, HHCl-Pi, HHCl-Po, and Residual-P) comprised over 75% of total phosphorus, followed by moderately labile phosphorus (NaOH-Pi, NaOH-Po, NaHCO₃-Pi, and NaHCO₃-Po) and labile phosphorus (Resin-P). Two-way ANOVA revealed that slope position, soil layer, and their interaction significantly affected soil phosphorus fractions (Table 1). Slope position significantly influenced stable phosphorus fractions, while soil layer significantly affected moderately labile phosphorus ($P < 0.05$). Their interaction significantly impacted stable phosphorus contents including HCl-Pi and Residual-P ($P < 0.05$).

In the crust layer, total phosphorus, organic phosphorus, inorganic phosphorus, and stable phosphorus contents were significantly higher at the slope bottom than on east and west slopes. Conversely, in the 0-5 cm soil layer, the west slope showed significantly lower values than the slope bottom and east slope ($P < 0.05$). The contents of NaOH-Pi and NaOH-Po were significantly higher on east and west slopes than at the slope bottom in the crust layer, while in the 0-5 cm soil layer, the west slope exhibited significantly higher values than the east slope and slope bottom (Figure 2).

2.2 Effects of Slope Position on Soil Enzyme Activities

Soil layer significantly affected ALP and GC activities, and the interaction between slope position and soil layer significantly influenced ALP activity (Table 1). Both enzyme activities were significantly higher in the crust layer than in the underlying 0-5 cm soil across all slope positions ($P < 0.05$). In the crust layer, ALP activity on the east slope was lower than on the west slope and slope bottom, though differences were not significant. In the 0-5 cm soil layer, the opposite pattern was observed, but differences remained non-significant ($P > 0.05$) (Figure 4).

2.3 Key Factors Influencing Soil Phosphorus Fractions

Correlation analysis revealed that soil moisture was significantly positively correlated with labile phosphorus and $\text{NaHCO}_3\text{-Po}$, but significantly negatively correlated with NaOH-Po and moderately labile phosphorus. Soil temperature was significantly negatively correlated with stable phosphorus, TP, and NaOH-Po , but positively correlated with $\text{NaHCO}_3\text{-Pi}$ and $\text{NaHCO}_3\text{-Po}$. Soil pH was significantly positively correlated with NaOH-Pi but negatively correlated with NaOH-Po and moderately labile phosphorus. Electrical conductivity was significantly positively correlated with NaOH-Pi and NaOH-Po , while biomass showed significant positive correlations with NaOH-Pi and NaOH-Po (Figure 5).

Random forest modeling identified key predictors of phosphorus fraction transformations (Figure 6). Soil moisture was the most critical variable affecting labile phosphorus transformation, followed by GC activity and $\text{NH}_4^+\text{-N}$ content. Ammonium nitrogen, pH, soil layer, and temperature were key variables influencing moderately labile phosphorus transformation. Temperature, slope position, and electrical conductivity significantly affected stable phosphorus transformation.

3.1 Effects of Slope Position on Lichen Crust Phosphorus Fractions

Consistent with our first hypothesis, slope position-induced variations in water and thermal conditions affected soil phosphorus fractions in lichen crusts. West slopes exhibited higher labile phosphorus content in the crust layer compared to east slopes, primarily because the hydrothermal conditions on west slopes were more favorable for lichen crust development, promoting phosphorus turnover. Although east slopes (as shady slopes) in the Gurbantunggut Desert have higher average soil moisture and lower temperatures, they are typically steeper as windward slopes. West slopes have higher soil clay content that enhances water retention and condensation water accumulation. Additionally, west slopes receive direct morning sunlight later, allowing biological soil crusts to better utilize early morning condensation water for growth—a phenomenon confirmed by previous studies showing significantly higher lichen crust biomass per unit area on west slopes compared to east slopes.

Beyond moisture, temperature differed substantially between slope positions. West slopes receive more solar radiation daily than east slopes. As heliophytic organisms, lichen crusts are influenced by slope aspect. Increased temperature enhances microbial activity and metabolic rates, providing abundant carbon sources that promote iron and aluminum oxide redox reactions (Fe^{3+} reduction to Fe^{2+}), facilitating transformation of stable phosphorus to bioavailable forms. The significant negative correlation between temperature and stable phosphorus in our results further demonstrates that warming promotes accumulation of available phosphorus.

Soil physicochemical properties are important factors influencing soil phosphorus cycling. Our results confirmed that pH, electrical conductivity, and other

properties at the slope bottom affected phosphorus fractions. Higher pH can cause soil acidification under certain conditions, promoting phosphorus binding with aluminum and iron to form insoluble compounds and reducing available phosphorus. However, pH reduction (toward neutral) in our study increased plant and microbial activity, promoting phosphorus turnover. The significant negative correlation between pH and $\text{NaHCO}_3\text{-Po}$, as well as with labile and moderately labile phosphorus, confirmed that pH reduction promoted accumulation of these fractions, particularly NaOH-Po . In alkaline soils, biological crust development lowers pH (near neutral), inhibiting Po mineralization processes. This may explain why NaOH-Po was the only fraction that did not increase in labile and moderately labile phosphorus pools.

3.2 Key Factors Influencing Lichen Crust Phosphorus Fractions

In arid and semi-arid regions, moisture is the primary limiting factor for plant growth. Lower-lying areas with higher soil moisture favor plant development and microbial community activity, enhancing phosphorus uptake and utilization by plants and microorganisms—similar to our findings. Our study also revealed that higher soil moisture at the slope bottom promoted lichen crust growth, which absorbed more bioavailable phosphorus, converting soil Pi into Po. High moisture also increased soil solution mobility, enhancing contact between phosphate and metal ions and promoting formation of stable and moderately labile phosphorus. Soil electrical conductivity also influenced phosphorus adsorption capacity. The significant positive correlation between EC and $\text{NaOH-Pi}/\text{NaOH-Po}$ indicated that EC affected phosphorus cycling through multiple pathways. In alkaline soils, abundant exchangeable calcium often combines with free inorganic phosphorus to form stable calcium-bound phosphates. EC reduction promotes conversion of these to labile and moderately labile forms but also increases iron and aluminum adsorption of phosphate, creating complex effects on phosphorus bioavailability.

4 Conclusion

Soil phosphorus fractions beneath lichen crusts in the Gurbantunggut Desert are dominated by stable phosphorus (HCl-Pi , HHCl-Pi , HHCl-Po , and Residual-P), comprising over 75% of total phosphorus. Slope position significantly affects soil phosphorus fraction contents through its influence on surface water and thermal conditions. In the crust layer, contents of TP, Po, Pi, and stable phosphorus were significantly higher at the slope bottom than on east and west slopes, while in the 0–5 cm soil layer, the west slope showed significantly lower values than the slope bottom and east slope. Random forest analysis indicated that labile phosphorus content was primarily influenced by soil moisture; moderately labile phosphorus was significantly affected by ammonium nitrogen, pH, soil layer, and temperature; and stable phosphorus was significantly impacted by temperature, slope position, and electrical conductivity.

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Note: Figure translations are in progress. See original paper for figures.

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